

# The Diets of Alaskan *Neptunea*

by

RONALD L. SHIMEK<sup>1</sup>

University of Alaska, Anchorage, and  
University of Washington, Friday Harbor Laboratories

**Abstract.** Diets of *Neptunea pribiloffensis*, *N. lyrata*, *N. heros*, and *N. ventricosa* from a series of subtidal sites in the Bering Sea, and *N. lyrata* and *N. pribiloffensis* from an intertidal habitat in south-central Alaska, were examined and compared. All species were found to feed primarily upon bivalves and polychaetes, secondarily upon carrion. *Neptunea pribiloffensis*, in particular, appears to feed on live polychaetes and bivalves. Other prey taxa are well represented in the diets of these large whelks.

In the Bering Sea, these four species are found in two paired groups. *Neptunea heros* and *N. ventricosa* are the more northern, colder-water pair, and *N. pribiloffensis* and *N. lyrata* are the southern, warmer-water pair. Diets of each species within each pair are similar and the pooled diets of both species within each pair are similar when both pairs are allopatric. When all four species are sympatric, the diets overlap significantly less. Similarly, the diets of *N. lyrata* and *N. pribiloffensis* from south-central Alaska overlap substantially with the diets of all four species from the non-overlap regions of the Bering Sea, but overlap significantly less with diets of all four species from the region of sympatry.

## INTRODUCTION

LARGE GASTROPODS of the family Buccinidae, often very abundant in north-temperate and boreal areas (PETERSEN, 1911a, b, 1913; BLEGVAD, 1914; NIELSEN, 1975; NAGAI & SUDA, 1976; PEREYRA *et al.*, 1976; TAYLOR, 1978; TAYLOR *et al.*, 1980), are presumed to be carrion feeders and facultative carnivores. Considering the diversity of the family (BAXTER, 1981) and the relatively large size and economic importance of the snails, however, their diets are relatively unknown (BLEGVAD, 1914; HUNT, 1925; AVERY, 1961; PEARCE & THORSON, 1967; VILLEMURE & LAMOUREUX, 1975; TAYLOR, 1978).

In the eastern Bering Sea and in south-central Alaska, the dominant marine gastropods, in size and biomass, belong to the buccinid genus *Neptunea*. *Neptunea* is circum-boreal, but has a center of distribution in the north-central Pacific-Bering Sea region (NELSON, 1978). The diet of the European *Neptunea antiqua* (Linnaeus, 1758) has been examined (PEARCE & THORSON, 1967; TAYLOR, 1978), but few feeding observations have been made for any of the Pacific species (AVERY, 1961). The four largest and most abundant species of *Neptunea* in the eastern Bering Sea are *N. lyrata* (Gmelin, 1791), *N. pribiloffensis* (Dall, 1919), *N. heros* (Gray, 1850), and *N. ventricosa* (Gmelin, 1791). Together with some other large gastropods, they

are the basis for a small pot fishery in the Bering Sea (MACINTOSH, 1978). In most Atlantic areas, however, buccinids have been considered an economic nuisance (PETERSEN, 1911b), although recently some attempts have been made to assess population sizes in anticipation of fisheries attempts (VILLEMURE & LAMOUREUX, 1975).

Information on the Bering Sea neptunes is fragmentary (PEREYRA *et al.*, 1976; MACINTOSH & PAUL, 1977); nonetheless, they are clearly an important component of that region's benthic fauna. The Bering Sea benthos consists of two major faunal assemblages, each somewhat correlated with depth, and certainly correlated with characteristic bottom-water temperatures. The low-Arctic-Boreal assemblage, found in the northwestern portions of the Bering Sea, is correlated with bottom temperatures exceeding 2°C only briefly in the summer, generally is found in depths in excess of 50 m, and contains *N. heros* and *N. ventricosa*. The Subarctic-Boreal assemblage, found in the southern and southeastern portions of the basin, exists where the bottom temperature is a relatively constant 2-4°C, is characteristic of shallow waters, and contains *N. lyrata* and *N. pribiloffensis* (NEIMAN, 1963; NAGAI & SUDA, 1976; PEREYRA *et al.*, 1976; MACINTOSH & PAUL, 1977). The replacement of one faunal assemblage by the other occurs in a transition zone often in excess of 50 km wide. With the exception of several cosmopolitan species, mainly polychaetes, most invertebrate benthic taxa are represented by different species in the two regions (NEIMAN, 1963).

<sup>1</sup> Mailing address: Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada.

Portions of the Subarctic-Boreal assemblage are found south of the Aleutians. In particular, *N. lyrata* and *N. pribiloffensis* have ranges extending to at least the Washington coast. They appear to follow a thermal gradient, for they are characteristically deep-water species there (RICE, 1972; ABBOTT, 1974). Both species are found intertidally in south-central Alaska. In some cases, they are the most abundant gastropods in the low intertidal zone (SHIMEK, 1981).

Buccinid gastropods are presumed to be primarily scavengers or carrion feeders. This assumption is based on three premises. Firstly, they lack the accessory boring organ found in the muricid gastropods; consequently, they are unable to attack efficiently bivalve or barnacle prey by boring. Secondly, they come readily to bait. And finally, those few whose diets have been examined have been shown to eat a wide variety of prey. Based on preliminary field observations, I hypothesized that Alaskan *Neptunea* are predatory and only rarely eat carrion. I asked the following questions. What is the diet of each species? Is there any specialization with regard to either prey taxon or prey guild? Can the food be characterized as having been alive or dead? What is the overlap in the diets of sympatric species? If they are predominantly scavengers, the dietary overlaps should be higher than if they are predators, assuming some predator-prey specialization. And, in areas of geographical overlap, are the diets of the species similar?

I examined gut contents of adults and large juveniles of the four *Neptunea* species. By identifying the snails' gut contents as precisely as possible, I hoped to determine their diets. *Neptunea* is a large genus containing many similar species (GOLIKOV, 1961, 1963; NELSON, 1978), and the radulae are similar and unspecialized in the species examined (KANG, 1976; Shimek, unpublished observations). Feeding structures are often strongly correlated with the prey taken, especially in specialized carnivorous gastropods (NYBAKKEN, 1970; NYBAKKEN & McDONALD, 1981; SHIMEK, 1983a), although the adaptive significance of some of these structures remains obscure. The similarities in the radulae and the similar gut morphologies of all four *Neptunea* species examined indicate prey items are probably captured and digested similarly in these species.

## MATERIALS AND METHODS

Bering Sea snails were collected using an Eastern otter trawl constructed with 10.2-cm mesh on the wings and body and 8.5-cm mesh in the intermediate section and cod-end. The cod-end was lined with 3.2-cm mesh. Few snails smaller than 50 mm in total length were collected. Furthermore, as the net's behavior on the bottom was unpredictable, the samples from different sites must be considered qualitative; however, they were assumed to be comparable. Trawl-collected animals were either preserved in 70% isopropyl alcohol or frozen. Trawl-collected

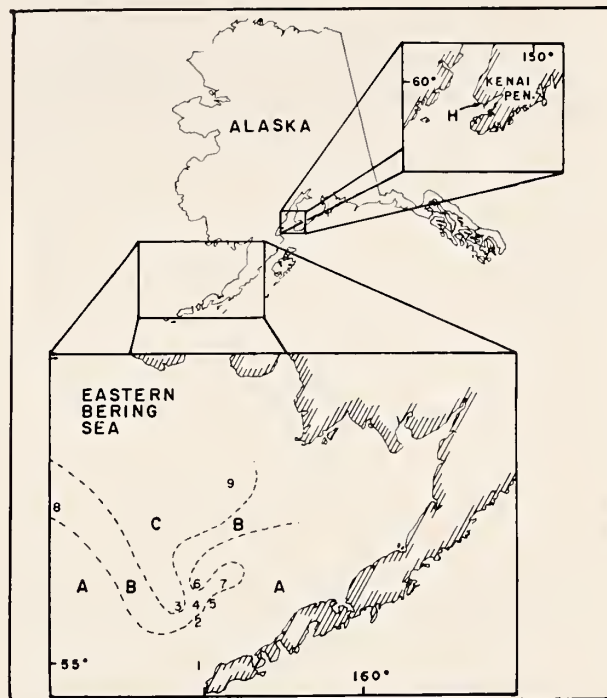


Figure 1

Map of Alaska showing snail collecting sites. A, region of *N. lyrata* and *N. pribiloffensis* pair only; B, region where all species are found; C, region of *N. heros* and *N. ventricosa* pair only; H, intertidal site near Homer, Alaska. Numbers refer to the collecting sites detailed in Table 1.

specimens came from several locations in the Bering Sea (Table 1, Figure 1).

Field observations were made on a mixed *N. lyrata*-*N. pribiloffensis* assemblage living on a low (-1.0 to -1.5 m below MLLW) intertidal sandstone bench near Homer, Alaska (59°38'N; 151°27'W), to determine feeding meth-

Table 1  
Bering Sea snail collection localities.

Area	Position	Number	Number collected			
			<i>Neptunea</i>			
			<i>lyr.</i>	<i>prib.</i>	<i>vent.</i>	<i>heros</i>
A	54°59'N; 165°09'W	1	18			
A	55°59'N; 165°10'W	2	116	38		
A	56°39'N; 165°09'W	6	2	1		
A	56°20'N; 164°35'W	5		48		
B	56°19'N; 165°12'W	4		34	21	
B	56°39'N; 164°13'W	7	45	7	68	14
B	57°39'N; 169°39'W	8				32
C	56°20'N; 165°47'W	3			63	
C	58°00'N; 164°01'W	9			54	100

Table 2

Gut contents of *Neptunea* species. \* = Some Homer *N. pribiloffensis* had more than one item in their guts.

Species:	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		TOTAL
Area:	A	B	H	A	B	H	B	C	B	C	
Contents:											
Hydrozoa								3	3		6
Polychaeta	7	14	29	14	2	3		12	1	13	95
Cirripedia				4			2	1	4	6	17
Decapoda	1				1						2
Bivalvia	9		28	26	1	7	7	8	3	21	110
Gastropoda							2				2
Ophiuroidea							1				1
Osteichthyes				1					1	1	3
Sand	14	9	23	25	3	12	5	11	3	16	121
Unidentified	3		26	6	6	5	5	16	20	9	96
TOTAL FEEDING	34	23	106 (98)*	76	13	27	22	51	35	66	453 (445)*
No contents	53	18	72	60	32	25	24	49	53	51	437
TOTAL	87	41	170	136	45	52	46	100	88	117	882

ods, and to assess the range of prey taken. Field-collected animals were frozen for later analysis. Band transects were done monthly from May through September, 1979, to assess the number of animals in each habitat.

Feeding animals were noted and their food was determined if possible. The intertidal bench was a heterogeneous area consisting of three major habitats: a silt-cov-

ered sandstone bench area, areas of cobble, and areas of dense mats of the sabellid polychaete *Schizobranchia insignis* Bush, 1904. Samples of the infauna were collected by recovering all of the sediment from 0.25-m<sup>2</sup> randomly placed quadrats in the worm-mat areas and the silt-covered inter-mat areas. Sediment collected for analysis was fixed for 24 h in 10% seawater-formalin, stained with

Table 3

Dietary overlaps of *Neptunea* species by area.

# Species—Area	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. <i>N. lyrata</i> —A		○	○	○	○	●	●	●	●	●
2. <i>N. pribiloffensis</i> —A	0.841		○	○	○	●	●	●	□	●
3. <i>N. pribiloffensis</i> —H	0.802	0.868		○	●	○	●	●	□	●
4. <i>N. ventricosa</i> —C	0.934	0.829	0.808		○	●	●	●	●	□
5. <i>N. lyrata</i> —H	0.922	0.829	0.791	0.812		●	●	●	□	□
6. <i>N. heros</i> —C	0.686	0.745	0.833	0.692	0.633		●	□	●	●
7. <i>N. lyrata</i> —B	0.561	0.721	0.750	0.567	0.550	0.750		□	□	●
8. <i>N. heros</i> —B	0.667	0.529	0.491	0.659	0.583	0.333	0.250		●	■
9. <i>N. ventricosa</i> —B	0.400	0.333	0.333	0.504	0.333	0.438	0.333	0.417		■
10. <i>N. pribiloffensis</i> —B	0.500	0.412	0.509	0.317	0.300	0.500	0.500	0.000	0.083	

Mean + 1 SD &lt; D &lt; Mean + 2 SD = 0.795–1.000 indicated by: ○

Mean D = 0.570 ± 0.224

Mean – 1 SD ≤ D ≤ Mean + 1 SD = 0.346–0.794 indicated by: ●

Mean – 2 SD &lt; D &lt; Mean – 1 SD = 0.121–0.345 indicated by: □

D &lt; Mean – 2 SD = 0.000–0.120 indicated by: ■

 $H_0: D_{Bi} > D_{jk}$  where  $i = A, B, C, H$ ; and where  $j, k = A, C, H$ .Mean  $D_{Bi} = 0.454 \pm 0.177$  N = 30Mean  $D_{jk} = 0.802 \pm 0.084$  N = 15Calculated  $t = 7.18$ , 43 d.f. $t_{0.001, 60} = 3.460$ ; therefore reject  $H_0$  with  $\alpha < 0.001$



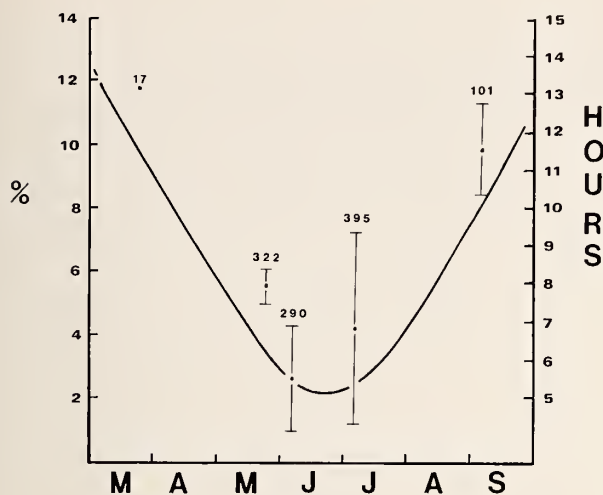


Figure 2

Relationship between percent of animals observed feeding (mean  $\pm$  1 SD) and the number of hours between sunset and dawn. Left ordinate gives percent feeding (●), where numbers indicate the number of snails examined during a given sampling period. Right ordinate gives hours between sunset and sunrise at this latitude (indicated by the solid line). Spearman Rank Correlation Coefficient between observed feeding percentage and sunset-sunrise time = 1.

Rose Bengal, and stored in 70% isopropyl alcohol. The sediment was sieved through 0.5-mm screens and animals retained on the screens were identified. Polychaetes and bivalves, potential prey, were identified to species; other taxa were generally identified to class.

Snails returned to the laboratory were removed from the shell, sexed, and the stomach and hindgut were examined for contents. Preliminary examination of the mouth and esophagus in 150 animals yielded no contents; thus, examination of the foregut was not done for the majority of the specimens. Gut contents were examined microscopically and identified if possible, using standard references. Results were analyzed using *t*-tests, and log-likelihood ratios (SOKAL & ROHLF, 1969). Similarity in diets was compared using the common lowest percentage or "D" index (SCHOENER, 1968).

## RESULTS

Gut contents of 128 *N. lyrata*, 181 *N. pribiloffensis*, 146 *N. heros*, and 205 *N. ventricosa* from the eastern Bering Sea were analyzed by area. Similarly, the gut contents of 52 *N. lyrata* and 170 *N. pribiloffensis* from the Homer area were examined (Table 2).

About half of the animals examined had empty guts. The others contained a wide variety of items, but generally the most abundant recognizable items were bivalve fragments (ctenidial remains, shell fragments, or cuticular siphonal coverings), polychaete remains (fragments with

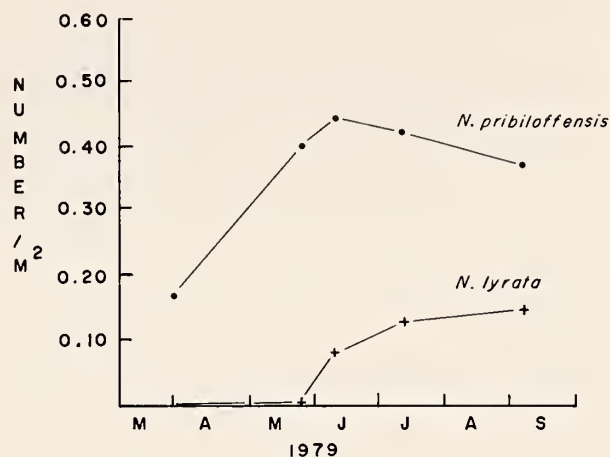


Figure 3

Observed abundance of *Neptunea* spp. at site H.

setae or whole worms), or barnacles (trabeculate plates, cirri, or entire animals except for the calcareous plates).

A large fraction of the contents consisted of sand and unidentifiable tissue fragments. These categories were excluded from the dietary overlap analyses. The absolute and relative frequencies of these categories varied from species to species, and within species from area to area.

Dietary overlap analyses were done using only the identifiable gut contents. To ensure consistency of interpretation, the general systematic category utilized was class (Table 2). Bering Sea snails exhibited substantial differences in diet within a species between areas of non-overlap (Areas A, C) and overlap (Area B, Table 3). *Neptunea lyrata* and *N. pribiloffensis* diets within area A overlap substantially, as do the diets of *N. heros* and *N. ventricosa* within area C. Furthermore, these two pairs of species have diets that overlap to a high degree (Table 3). The diets from area B are much less similar. There is a general trend for any species' diet in the overlap area to be different from its diet in either area A or C. There is also high overlap between the diets of *N. lyrata* and *N. pribiloffensis* from the Homer area, and these diets are similar to the diets of the respective species from area A. The mean dietary overlap for all species combinations between and within areas A, C, and H is significantly higher than the mean dietary overlap for all species combinations between areas A and B, C and B, H and B, and all species combinations within area B (Table 3).

Field observations of feeding at Homer generally confirm the diet as consisting of either polychaetes or bivalves, although the fraction of snails feeding is very low compared to the fraction with food in their guts (Table 4). The number and fraction of *N. pribiloffensis* observed feeding varied monthly, and were highly correlated with the amount of time between sunset and sunrise, indicating that feeding is largely nocturnal, at least intertidally (Figure 2).

Table 4

Frequency of dietary items. \* = More than one food item per snail for some categories.

Species: Area:	Gut contents										Field feeding observations	
	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		<i>N. pribiloffensis</i>	<i>N. lyrata</i>
	A	B	H	A	B	H	B	C	B	C		
Contents:												
Hydrozoa								0.03	0.03			
Polychaeta	0.08	0.34	0.18	0.10	0.18	0.06		0.12	0.01	0.11	0.02	0.01
Cirripedia				0.01			0.04		0.03	0.05		
Decapoda	0.01				0.02						<0.01	
Bivalvia	0.10		0.16	0.21	0.02	0.13	0.15	0.08	0.03	0.17	0.02	0.03
Gastropoda							0.04					
Ophiuroidea							0.02					
Osteichthyes				0.01					0.01	0.01		
Sand	0.16	0.22	0.14	0.18	0.07	0.23	0.11	0.11	0.03	0.14		
Unidentified	0.03		0.15	0.04	0.13	0.10	0.11	0.16	0.23	0.08		
Nothing	0.61	0.44	0.42	0.44	0.71	0.48	0.52	0.49	0.60	0.44	0.95	0.97
TOTAL	0.99	1.00	1.05*	0.99	0.99	1.00	0.99	0.99	0.97	1.00	0.99	1.01
Number	87	41	170	136	45	52	46	100	88	117	1125	185

Estimates of prey availability are not present for the Bering Sea populations, but are available for the intertidal population (Table 5). The sabellid *Schizobranchia insignis*, the relatively large rock-burrowing bivalve *Zirfaea pilsbryi* Lowe, 1931, and polychaetes in general are abundant.

Carion suitable for scavengers was seen occasionally, but was too rare for quantitative abundance estimates to be meaningful. Both species of *Neptunea* were relatively abundant in this intertidal area (Figure 3).

Only within the Polychaeta was prey discrimination to

Table 5

Infaunal organisms at Homer area.

Taxon	Mean number per m <sup>2</sup> ± 1 SD			
	May		September	
	Worm mat	Bare bench	Worm mat	Bare bench
Cnidaria		525 ± 742		3175 ± 601
Phoronida		20 ± 6		8 ± 11
Priapulida		8 ± 11		
Annelida				
Oligochaeta	18,800 ± 3191	2019 ± 547	20,000 ± 20,365	1050 ± 212
Polychaeta				
Maldanidae	6756 ± 470	16 ± 23	5350 ± 1061	125 ± 106
Nephtyidae	40 ± 11	31 ± 1	400 ± 424	
Nereidae	46 ± 3	600 ± 34	650 ± 261	220 ± 28
Pectinariidae			900 ± 849	
Polynoidae	230 ± 14	367 ± 58	200 ± 282	
Sabellidae	41,598 ± 1536	15,385 ± 5071	16,250 ± 1060	50 ± 72
Others	7677 ± 1747	15,385 ± 4606	23,050 ± 1095	83,320 ± 45,368
Mollusca				
Bivalvia				
<i>Zirfaea pilsbryi</i>	22 ± 19	23 ± 37	22 ± 35	20 ± 24
Others	3893 ± 1121	600 ± 237	10,300 ± 1229	1678 ± 2011
Gastropoda	186 ± 32	238 ± 274		
Arthropoda	3406 ± 1491	13,270 ± 4624	15,300 ± 6075	11,050 ± 1485
Echinodermata			50 ± 71	
TOTAL	86,654 ± 13,448	48,448 ± 6856	94,472 ± 16,663	100,621 ± 20,743

Table 6  
Polychaete prey of *Neptunea*.

Species:	<i>N. pribiloffensis</i>			<i>N. lyrata</i>			<i>N. heros</i>		<i>N. ventricosa</i>		TOTAL
Area:	H	A	B	H	A	B	B	C	B	C	
Family:											
Spionidae	2									1	3
Cirratulidae			2		3			8		6	19
Maldanidae	1	1	9	1	2					1	15
Polynoidae				1							1
Nereidae	2										2
Nephtyidae	3										3
Sabelliidae	2										2
Pectinariidae	1										1
Ampharetidae								2			2
Terebellidae		3			1			1		1	6
Sabellidae	20		1	1	2					3	27
Unidentified	0	2	2	0	6	2	0	12	1	13	39
TOTAL	31	7	14	3	14	2	0	23	1	25	120

a systematic category lower than class possible. Polychaete remains were generally identifiable to family and occasionally to species, although the lack of specimens for confirmational comparison of setal morphologies from the Bering Sea areas makes the latter identifications somewhat doubtful. Some similarity is seen in the polychaete prey taken when considered area by area (Table 6). Errant polychaetes, absent from the guts of the Bering Sea snails, were commonly found in the guts from the Homer *N. pribiloffensis*. Maldanids seemed to be a favored food for *N. lyrata* and *N. pribiloffensis*, whereas cirratulids were taken more frequently by *N. heros* and *N. ventricosa*.

## DISCUSSION

The large *Neptunea* species of the eastern Bering Sea and south-central Alaska are clearly divisible into two groups of species pairs of similar dietary and habitat utilizations. When the two groups are allopatric, the northern, colder-water pair, *N. heros* and *N. ventricosa*, has a high dietary overlap with the southern group, *N. lyrata* and *N. pribiloffensis*. The benthic fauna in the Bering Sea is characterized by a few widely spread assemblages and a larger number of smaller, more local ones (NEIMAN, 1963). Replacement of one major assemblage by another is gradual, and is often accomplished by the replacement of one species by another similar species (i.e., *N. heros* by *N. lyrata*; *N. ventricosa* by *N. pribiloffensis*) rather than by wholesale changes in the character of the fauna (NEIMAN, 1963). Quantitative data for changes in the infauna in this region are not available, but given the noted gradual changes in the epifauna (PEREYRA *et al.*, 1976) and similar qualitative observations about the infauna (NEIMAN, 1963), it is reasonable to infer that the composition of the infauna at the class level is relatively consistent.

The dietary similarity between the Homer and Bering

Sea populations of the *N. lyrata*-*N. pribiloffensis* group strengthens the argument that this pair of species chooses similar prey categories wherever it is found. The two habitats are strikingly different; the Homer area is a rocky sandstone beach, whereas the Bering Sea area A is a relatively flat sandy subtidal plain, yet the diets show a high degree of overlap at the class level.

If scavenging is defined as eating carrion, then tubicolous polychaetes and bivalves are unlikely items to be represented in the diets of scavengers. Both prey types bury in the substrate and upon death are immediately covered by sediment. *Neptunea* could be scavenging food, however, from the remains of some other organisms' meals. The presence of entire polychaetes and barnacles, and, effectively, the remains of entire gastropods (no shell); the remains were macerated, but substantially complete) argue against this. Furthermore, field feeding observations indicated *N. pribiloffensis* and *N. lyrata* can easily eat large bivalves that cannot close their shells completely.

The piddock *Zirfaea pilsbryi* is commonly found burrowed into the sandstone of the Homer area. Both *Neptunea* species feed on it by extending their proboscides down the siphon and rasping away the flesh of the body. A specimen of *Neptunea pribiloffensis* with a shell length of 40 mm can extend its proboscis over 35 cm, allowing easy feeding on buried infauna. In the Bering Sea samples, many of the bivalve remains contained rolled masses of cuticle, which when unrolled were obviously the cuticular coverings from clam siphons similar to the siphons of *Mya*. *Mya* species gape; and *Mya truncata*, a common arctic bivalve, is present in the Bering Sea (NEIMAN, 1963; ABBOTT, 1974).

In the Homer area, many individuals of *N. pribiloffensis* were seen feeding similarly on the sabellid polychaete *Schizobranchia insignis*. They would extend their proboscides into the polychaete tubes and eat the worms. The



worms are gregarious and their tubes often tightly intertwine. It is likely that worms adjacent to the one whose tube was initially penetrated also are eaten. As many as five specimens of *S. insignis* were found in the gut of one *N. pribiloffensis*. Other polychaetes were taken by *N. pribiloffensis*, and these prey do not appear to be randomly selected, as some taxa eaten are rare in the sediment samples. The significance of these choices remains unclear. *Neptunea pribiloffensis* is clearly adept at capturing errant as well as tubicolous sedentary worms, indicating that this species in particular can be a predator on mobile prey.

The analysis of the polychaete prey also shows that the similarities seen in diets are to some extent an artifact of the analysis. Within the class Polychaeta, the prey taken are distributed among 11 families and probably more than 20 species. Thus, although these whelks form a predatory guild adapted to exploiting polychaetes and bivalves, it is unlikely that they are in direct competition with one another for any one species of prey.

Bivalves have been shown to be important dietary components in these (present study) and other *Neptunea* (BLEGVAD, 1914; PEARCE & THORSON, 1967; TAYLOR, 1978), and I suspect both the sand and unidentified tissue remains to be primarily the result of consuming bivalves. Bivalve tissues have few overt structural clues as to taxonomic origin and, thus, are difficult to identify when partially digested. The dense sand probably passes through the guts of *Neptunea* slower than most tissue fragments, resulting in some specimens containing only sand in their guts. In many specimens, gut contents clearly identifiable as being of bivalve origin contained a large fraction of sand in the midgut and unidentifiable tissue fragments in the hindgut. In most cases then, the categories of sand and unidentifiable tissue fragments probably represent the remains of deposit-feeding bivalves, or bivalves that inadvertently ingested sediment. Items clearly dead when eaten were a small constant dietary fraction for all four species. These items included fish remains (scales and tissue), king crab (*Paralithodes* sp.) remains (a dactyl), and a complete pandalid shrimp molt. The ophiuroid remains collected in one *N. heros* included only fragments of one ray, and may indicate scavenging. In the intertidal area, no *N. lyrata* and only one of 1125 *N. pribiloffensis* were observed eating carrion, a small dead *Cancer magister*.

### CONCLUSIONS

Neptunoid gastropods must be considered to be primarily predators on live prey, not scavengers or carrion feeders. This conclusion is supported by the predominance of live food in the diet and the dietary shift seen in the overlap zone. The distribution of carrion should be relatively independent if viewed at the class level, providing the faunal assemblages are generally comparable. The array of utilized prey is less diverse than the array of potential prey in the Homer area, indicating specialization on the described prey. The dietary shifts would be expected when

two food-limited systems overlapped, as each competing species pair was forced to utilize a more diverse, but less desirable suite of food, although it is unlikely that direct competition exists for any one prey species.

These four species exist as two paired species guilds adapted for exploitation of deeply dwelling or large infauna, although they are not bound to the resource. The extremely long proboscides of these snails are probably the major structural adaptations allowing exploitation of the large bivalves and tubicolous polychaetes as major resources. The snails are morphologically very similar and the diets within each guild are also quite similar. They are, however, reproductively isolated; each species has distinctly different egg capsules (GOLIKOV, 1963; SHIMEK, 1981). Predation on boreal soft-sediment infauna is uncommon among large prosobranchs. The naticids appear to be the only other successful group of large snails to exploit this resource. Because of their ability to bore shells, the naticids are apparently specialists on mollusks. The neptunoids exploit a wider array of potential prey, including polychaetes and cirripedes. In most soft-sediment communities, polychaetes are a major constituent in terms of species number, absolute number, and biomass. The polychaetes harvested by these *Neptunea* are large, although the juveniles probably take smaller worms.

Soft-sediment vermivory is best exemplified in prosobranchs by the immensely large and successful family Turridae (SHIMEK & KOHN, 1981; SHIMEK, 1983a, b, c), but the turrids in the north-central and north-eastern Pacific are generally small. These small snails, primarily in the genus *Oenopota*, appear to be largely specialist vermivores (SHIMEK, 1983c). *Oenopota* species are abundant and common in Alaskan waters (BAXTER, 1981), and neptunoids may have faced substantial competitive pressure, which forced them away from specialization on polychaetes. Moreover, the large size of the neptunoids may require more energy input per unit time than a steady diet of small polychaetes alone can provide.

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